THE MACARONESIAN CAVE-DWELLING SPIDER FAUNA (ARACHNIDA: ARANEAE)

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The composition of the cave-dwelling spider fauna of the Macaronesian Islands–Madeira, the Azores and the Canary Islands–is compared with the endemic epigean spider fauna of these archipelagos. The grades of adaptations in the cave-dwelling spiders are compiled, and the following questions are discussed: from which geographic regions did the stem species come? What can be said about the evolution of the species? How old are the cave-dwelling spider species?

Die Fauna der Höhlenspinnen der Makaronesischen Inseln - Madeira, Azoren und Kanarische Inseln- wird mit der endemischen epigäischen Fauna dieser Archipele verglichen. Der Grad der Anpassung an das Höhlenleben wird untersucht und verglichen; die folgenden Fragen werden diskutiert: Wo liegt der Ursprung der Stammarten? Was kann über die Evolution und das Alter der höhlen-bewohnenden Arten gesagt werden?□*Araneae, troglobites, Canarian and Macaronesian Islands, Island biology, biogeography, evolution.*

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Some island groups in the northern Atlantic–the Canary Islands, the Azores, the Archipelago of Madeira, the small Ilhas Selvagens and by most authors (but not by me) the Cape Verde Islands–are called Macaronesian Islands (Fig. 1). The Macaronesian Islands are mainly of volcanic origin, only the Eastern Islands (Fuerteventura, Lanzarote) are partly of continental origin and have been probably connected with Africa some million years ago.

The first troglophilic and troglobitic Macaronesian spiders were described in 1985 from Tenerife. Now cave-dwellers are known from Madeira (1 species), from the Azores (1 species) and from the Canary Islands (at least 17 endemic species, see Wunderlich, 1991), by far most species are known from Tenerife: at least 11 species = 10% of the endemics (and perhaps there are hundreds of mostly undescribed insect species of different orders).

Especially on the Canary Islands there are many caves. The best studied system of caves on Tenerife - cueva del Viento, cueva Reventon - is more than 16km long; the length of all Macaronesian caves is perhaps more than 100km, and only a few have been examined intensively.

MACARONESIAN CAVE-DWELLING SPIDERS

Nearly all cave-dwelling spiders are endemics of one island or even only one cave (Table 1):

Three species of those listed (Table 1) are not restricted to a single island:

1. *Meta bourneti* Simon, 1929 (Tetragnathidae) is a west-palearctic species introduced to a cave on Tenerife (Canary Islands);

2. *Agraecina canariensis* Wunderlich, 1991 (Liocranidae) is known from caves on Gran Canaria and Tenerife (Canary Islands);

3. *Rugathodes pico* (Merrett and Ashmole, 1989) (Theridiidae) is known from caves on Pico and Fajal (Azores).

Here I deal with five questions: 1. What is the composition of the Macaronesian fauna of troglophilic and troglobitic spiders and what are the differences to the epigean fauna? 2. Which species are extremely well adapted as cave-dwellers? 3. From which geographic regions did the stem species come? 4. What can be said about the evolution of the species? 5. How old are the cave-dwelling spider species?

Cave-Dwelling and Epigean Spiders

The most diverse spider families are shown in Figs 2-3. In the Canarian troglophilic and troglobitic cave-dwellers (Fig. 2): Dysderidae (at least 35%), Linyphiidae (25%) and Pholcidae (25%), the sum of these 3 families is 85%. (No Oecobiidae).

In the epigean endemic species (Fig. 3) the composition is quite different: Dysderidae 16%, Linyphiidae 15%, Pholcidae 13%, the sum of these 3 families is 44%, only half compared with the cave-dwellers. In the families Dysderidae

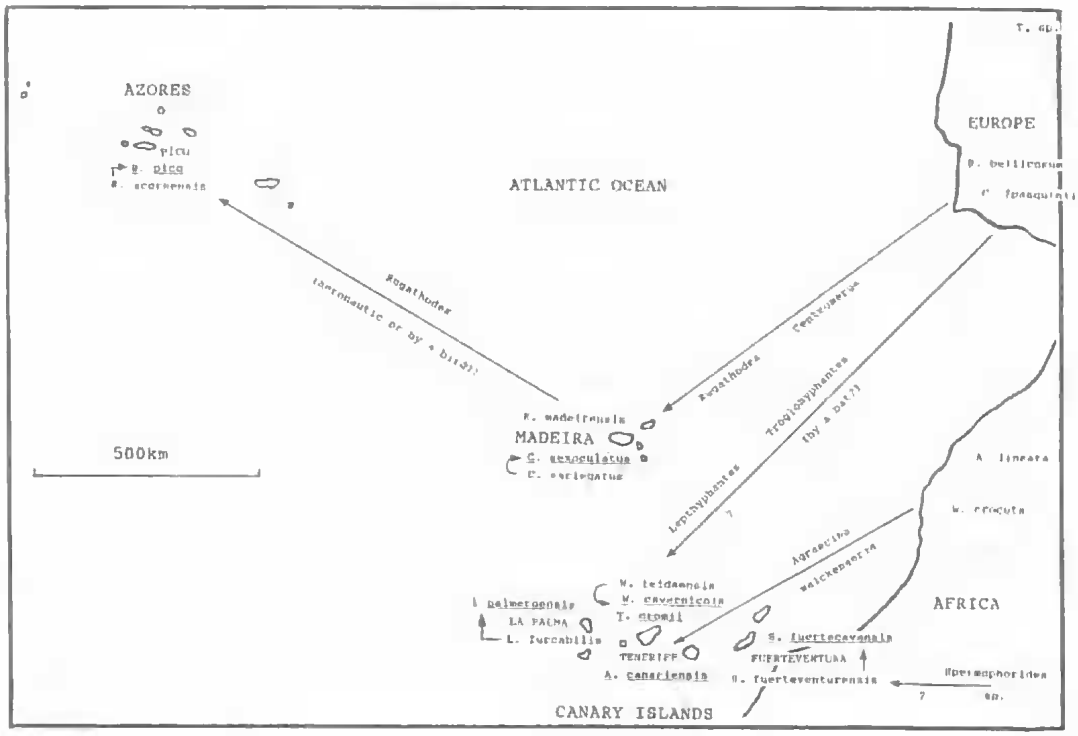


FIG. 1. The Macaronesian Archipelagos. Some Macaronesian cave-dwelling spiders (underlined) and their European and Macaronesian relatives.

(only *Dysdera*) and Pholcidae (*Pholcus* and *Spermophorides*) *all* epigean genera have evolved cave-dwelling species; in the Linyphiidae only members of 5 from 21 genera with endemic species have evolved cave-dwellers (= 25%). *Dysdera* is the genus richest in species in caves and out of caves on the Canarian and Maearonesian Islands. Oecobiidae probably do not find their prey -ants- in the caves.

Highly Adapted Cave-dwellers?

Different grades of adaptation to cave life in the Macaronesian spiders is evident in three structures (Table 1): the size of the eye lenses, the body pigmentation and length and slenderness of legs.

Some true cave spiders of *Dysdera* have reduced eyes, but neither depigmentation nor long and slender legs. I do not know the explanation. Thus, perhaps the eye reduction is the best indieator regarding the grade of adaptation to cave life in spiders. For diseussion below I ehoose the following five spider species.

1. *Meta bourneti* (Tetragnathidae, Tenerife) is restricted to deeper parts of caves, but the eyes are not redueed, the body is only slightly depigmented, and the legs are nearly of normal length. This species has been introduced from Europe or North Africa.

2. Not strongly adapted is *Agraecina canariensis*, but very variable in the depigmentation and in eye reduction (grades 1-3, Figs 4- 5). The variation is intrapopular. This seemingly troglophilic subterranean species is not restricted to caves.

3. In four Canarian species of *Spermophorides*, the eyes are more or less reduced (Figs 8-11); the eyes of an epigean *Spermophorides* sp. from Tenerife are normal (Fig. 12). Cave-dwelling *Spermophorides* spp. are not strongly related. The known species occur on four different islands. So the eye reduction must have been evolved independently four times.

4. *Rugathodes pico* is restrieted to caves. The spiders are strongly depigmented, they have strongly reduced eyes and the legs are long and slender (grades 3-4, Fig. 6a; cf. Fig. 6b the related epigean *R. acoreensis*).

5. In *Troglohyphantes oromii* (Ribera and Blasco, 1986) (Linyphiidae, Tenerife), the eyes are tiny or eompletely absent (Fig. 13), body and legs

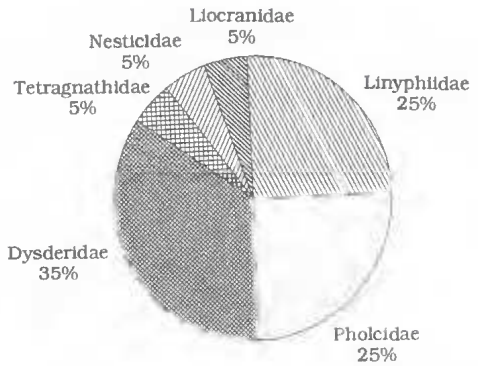


FIG. 2. Composition of Canarian families of troglophilic and troglobitic spiders based on 18 species.

are completely depigmented, the legs are very long and slender (all grades between 3 and 4). The adaptations in *Canarionesticus quadridentatus* (Nesticidae, Tenerife) and in *?Metopobactrus cavernicola* (Linyphiidae, Tenerife) are similar. These species show the strongest adaptations to cave life.

Origin of the Stem Species

Macaronesian cave-dwelling neoendemic spiders and their European relatives. The hypothetical origin of all species is the West-Mediterranean area, most came from Europe (Fig. 1), e.g. species of *Rugathodes* to the Azores - Madeira seems to be a 'stepping stone', *Centromerus* to Madeira. *Troglohyphantes* came perhaps from Spain to Tenerife, but the sister species is unknown. *Walckenaeria* came from North Africa to Tenerife, *Agraecina* came from Europe or North Africa to Tenerife (and Gran Canaria).

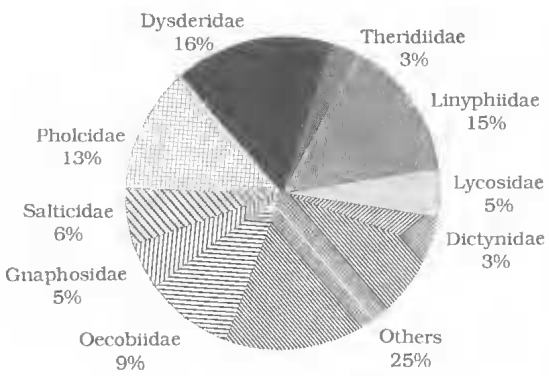


FIG. 3. Composition of Canarian families of *epigean* spiders based on more than 400 species.

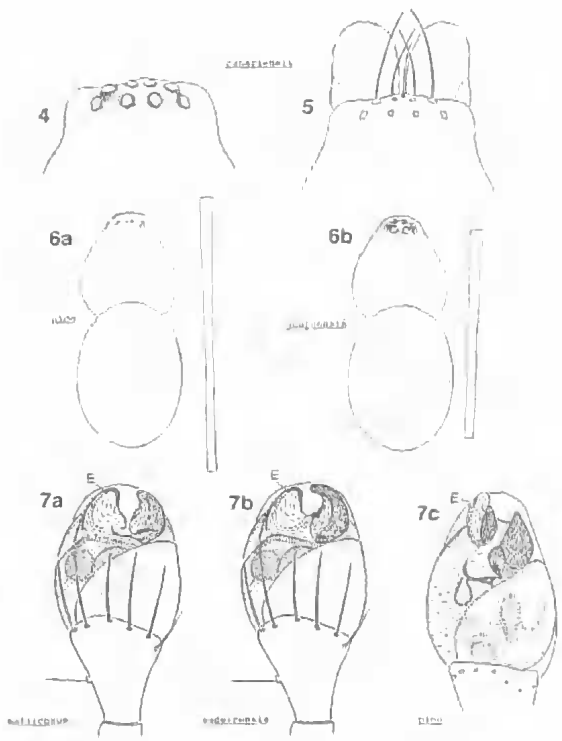
Species	Di	R.E.	Dep	Leg	T
Meto bourneti	Wpal,T	0	≤1	≤1	<2
Agraecina canariensis	Cl (GC,T)	0-3	0-3	1	1-7
Dysdera lobradaensis	Cl (T)	2	0	0	2
D. ratanensis	Cl (LP)	2	0	0	2
Lepthyphantes palmeraensis	Cl (LP)	1	1	1	3
D. chioensis	Cl (T)	3	0	1	4
D. ambulotenta	Cl (T)	3-4	0	0	3-4
Phalcus boldiasensis	Cl (T)	2	3	0	5
Spermophorides flovo	Cl (GC)	2	3	1	6
S. reventani	Cl (T)	1-2	1	2	≤5
D. esquiveli	Cl (T)	?3-4	1	1?	≥5
S. fuerteventurensis	Cl (F)	2	3	≤1	≤6
Wolckenaeria covernicolo	Cl (T)	1-2	1-2	3	6
S. justai	Cl (EH)	2-3	3	3	≤9
D. unguimmonis	Cl (T)	4	2-3	≤4	~10
Centromerus sexoculotus	M	3	4	2-3	≤10
Rugathodes pica	AZ	3	3	3-4	≤10
?Metopoboctrus covernicala	Cl (T)	3-4	3	3-4	~10
Troglahyphantes aromii	Cl (T)	3-4	4	3-4	~11
Canorionesticus quadridentotus	Cl (T)	4	3	4	11

TABLE 1. The Macaronesian troglophilic (at least the first two and perhaps the first five species) and troglobitic spider species and the grades of their adaptations from 0 (normal structures as in epigean taxa) to 4 (= eyeless or almost so/ completely depigmented/ very long legs, the species listed below); AZ = Azores, Cl = Canary Islands, EH = El Hierro, F = Fuerteventura, GC = Gran Canaria, LP = La Palma, M = Madeira, T = Tenerife, Wpal = West Palearctic). Di, distribution; R.E., reduced eyes, Dep, depigmentation; Leg, long & slender legs; T, Total.

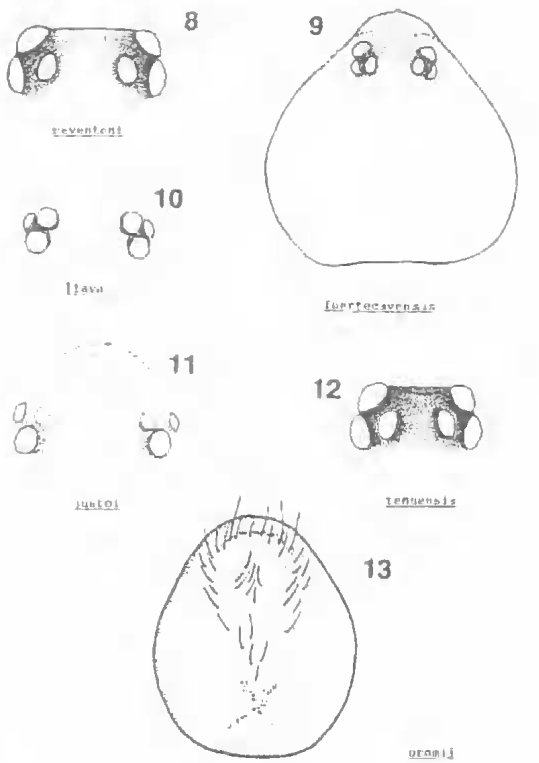
The occurrence of cave-dwelling species of the different genera on *Tenerife* - e.g. *Walckenaeria*, *Troglohyphantes* and *Agraecina* - are remarkable (Fig. 1). The highest Macaronesian mountain, the 3718m high Teide on Tenerife, seems to be a 'catcher' of aeronautic (ballooning) spiders which came from the Western Mediterranean area. This finding is supported by the relationships of the endemic spider fauna of the Teide and the Cañadas, an area surrounding this high mountain (cf. Wunderlich, 1991: 104-107).

Evolution of Macaronesian Cave-dwelling Spiders

In some spiders, e.g. *Canarionesticus quadridentatus* and *Troglohyphantes oromii*, no related epigean species is known, and almost nothing can be concluded about their evolution.



FIGS 4-7. 4-5. Variable eye reduction in subterranean Canarian *Agraecina canariensis* Wunderlich, 1991 (Liocranidae). 6, 7. *Rugathodes*. 6, ♂ body with eyes and right tibia 1 from the Azores: 6a, of the cave-dwelling *R. pico*; 6b, of the epigean *R. acoreensis*. 7. Right male pedipalps ventral: 7a, *R. bellicosum* (Simon, 1873), Europe; 7b, *R. madeirensis* Wunderlich, 1987, Madeira; 7c, *R. pico* (cavernicolous) and *R. acoreensis* (epigean), Azores. These species show no differences. (E = embolus).



FIGS 8-11. Eye reduction in Canarian cave-dwellers spiders: 8, *Spermophorides reventoni* Wunderlich, 1991; Fig. 9, *S. fuertecavensis*; 10, *S. flava* Wunderlich, 1991; 11, *S. justoi* Wunderlich, 1991. 12. Eyes of the epigean *S. tenoensis* Wunderlich, 1991, Tenerife. 13. Sometimes completely eyeless prosoma of cave-dwelling *Troglohyphantes oromii*, Tenerife.

(Several species are not well studied, e.g. *Dysdera* species, or only one sex is known). In this connection *Troglohyphantes oromii* is of special interest because nearly all species of this genus are troglophilic or troglobitic cave-dwellers as well as the species from Tenerife. I can imagine that there has never existed an epigean stem species on Tenerife and that the ancestors, perhaps as a cocoon, has been transported by a bat directly from a European cave to a cave on Tenerife. Several species or subspecies of bats fly from Europe via Madeira to the Canary Islands (Dr. Biscoito, Mus. Munic. Funchal, Madeira, pers. comm.). This hypothesis would explain why there is no epigean *Troglohyphantes* spp. on Tenerife or another Canary or Macaronesian Island. Otherwise I do not want to exclude the possibility that this species is a paleoendemic relict (Peck, 1990: 372-373).

Based on the very similar genital organ, in *Rugathodes pico* and *acoreensis* they are identical, I found some strongly related spider species (Table 3). In the cave-dwelling *R. pico* (Table 1 and discussed above), the adaptations to cave life and the differences in some non-genital structures compared with epigean species are very distinct: the eye reduction, the depigmentation and the prolongation of the legs, Fig. 6a; compare Fig. 6b of the epigean species, which is also known from the Azores. Otherwise the genital structures in the two Azorean species show *no* differences in both sexes (Fig. 7c), but there are distinct differences to *madeirensis* from Madeira (Fig. 7b) and *bellicosum* from Europe (Fig. 7a). So I do believe that *R. pico* and *R. acoreensis* are true sibling

Introduced species	Paleaoendemic species	Neoendemics
Meta bourneti	*Canarionesticus quadridentatus* (Nesticidae, Tenerife). No known relative.	The epigean sibling or sister species/stem species is known, usually from same island. To this group belong most Macaronesian cave spiders, see below (genesis/evolution). Dysderidae, Pholcidae, Linyphiidae, Theridiidae and Liocranidae.

TABLE 2. Historical groups of Macaronesian cave-dwelling spiders. Position of *Troglohyphantes oromii* in list is uncertain; it has no known epigean relative. See below: possible transport by a bat.

species (or even subspecies?) and that *R. acoreensis* also is the stem species of *R. pico*.

In *Spermophorides*, differences in genital and non-genital structures are distinct in both sexes, and perhaps they are not sister species. The remaining species in this list are known only from females.

Martin *et al.* (1989) assume that some Canarian troglobites can be considered as relict species which evolved after changes in the climate 'since there have been alternating wet and dry periods ... causing important changes in the fragile insular ecosystem on the surface.' (See below: *Rugathodes*). Furthermore the yearly seasonal changes–hot and dry summers, cooler and more humid winters especially on the Eastern Canary Islands–did perhaps initiate vertical movement of some species into the ground in the summer and also autecological changes for instance in *Centromerus fuerteventurensis* Wunderlich, 1991 (Linyphiidae). In this species, which is not a cave-dweller, the eyes are reduced as well as in species of *Scotargus* (Linyphiidae) and *Altella* (Dictynidae) of other Canarian islands (Wunderlich, 1991).

Borges and Oromi (1991) do prefer the "adaptive shifting theory" of Howarth (1973). 'This theory does not invoke isolation during climatic (or volcanic?) changes but instead proposes that the partly adapted ancestors shifted into newly developed niches.' In my opinion this theory can well explain the genesis of some Macaronesian cave-dwelling spider species including the ones listed above (see Peck, 1990: 366-368). Especially there exists large caves and lava tubes on the Canary Islands, and there are many ecological niches.

From the Macaronesian Islands and its spiders I know three kinds of preadaptations which support the 'adaptive shifting theory':

1. A lot of Canarian species are known as hypogean spiders and were caught using special traps in the ground in the so-called 'mesocavernous shallow stratum' (Wunderlich, 1991: 11). From this stratum and from accidental captures under stones I know Canarian species of *Dysdera*, *Spermophorides*, *Lepthyphantes*, *Walckenaeria*, *Altella*, *Zimirina* and others. These spiders have moderately reduced eyes and are more or less depigmented, they seem to be troglophilous and not macrocavernicolous, but microcavernicolous or myrmecophilous. *Agraecina canariensis* is a species of this stratum but it also penetrates caves. (A closely related species has been newly discovered in a Romanian cave).

2. Another preadaptation is offered in the conditions in the laurisilva (the relict laurel forest): high humidity and low changes in temperature. For example I found the laurisilva species *Troglonata madeirensis* Wunderlich, 1987 (Anapidae s.l.) in the wet and light part near the entrance of a cave on Madeira (Sao Vincente). I collected ♂ ♀ of *Lepthyphantes mauli* Wunderlich, 1991 (Linyphiidae) in the same part of this cave; this species probably also came from the wet forest near the cave.

3. The third kind of biotopes that lead to troglobitic conditions are under stones and under leaves on trees at places with a high humidity near stretches of water. At such places, under stones as well as under leaves on trees, I found on the Azores *R. acoreensis*, the epigean sibling/stem species of the cave-dwelling *R. pico*. Under a stone over flowing water on Tenerife I found partly depigmented spiders of *Walckenaeria alba*.

Age of Macaronesian Cave-dwelling Spider Species

The age of the Macaronesian caves remains unknown. The youngest Macaronesian Islands, the Western Azorean and the Western Canarian Islands, are only very few (1-2?) million years old. Two spider species, *Pholcus roquensis* and *Walckenaeria cavernicola*, are cave-dwellers at the Cañadas on Tenerife. The greatest age of these species could be the same as the age of this part of Tenerife, at least 200 000 (up to 2 million) years.

Rugathodes pico is known only from caves of the Azorean islands Pico (a young island) and Fajal. After Ashmole (in litt. 1991) these Azorean

Cave-dwelling species	Epigean relatives	Island	Family
Spermaphorides fuertecavensis	*S. ?fuerteventurensis*	Fuerteventura (Canary Is.)	Pholcidae
Centromerus sexoculatus, and sp. nov.	*C. variegatus*	Madeira	Linyphiidae
Lepthyphantes palmeraensis	*L.furcabilis*	La Palma (Canary Is.)	Linyphiidae
Walckenaeria cavernicola	*W.teideensis*	Tenerife (Canary Is.)	Linyphiidae
Rugathodes pico	*R.acareensisi*	Pico and Fajal (Azores)	Theridiidae

TABLE 3. Macaronesian cave-dwelling troglophilic or troglobitic spiders and their nearest epigean relatives, possible stem/ sister/sibling species from same island.

Islands had perhaps a land bridge during the last glaciation. So this species probably evolved from its closely related epigean stem species, near or identical with *R. acoreensis*, perhaps not later than 10 000 years ago (= 10 000 generations). From genital structures, in both sexes there are no differences, speciation should have happened, geologically, not long ago, that means at the end of the last glaciation. But this idea is very vague; perhaps the speciation happened much later, and *R. pico* was transported by bats from one island to the other only very few thousand years ago (Wunderlich, 1991: 200-201). Wunderlich (1991) gives further details of these cave-dwelling spiders and their taxonomy.

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